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BOTANICAL GAZETTE

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AN ECOLOGIC STUDY OF THE FLORA OF MOUNTAINOUS NORTH CAROLINA.

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TOPOGRAPHY.

THE mountain region of North Carolina is not a unit, dominated by a single range or group of mountains, but is a complex containing several features of nearly equal topographic importance. These are (1) the Blue Ridge, (2) the eastern Monadnocks and Piedmont valleys, (3) the Unaka Range, (4) the central mountain groups and intermontane valleys.¹

The Blue Ridge.—The Blue Ridge may be regarded as forming the extreme eastern range of the Appalachian Mountains, carrying the main divide between the Atlantic and Gulf drainage. It reaches its greatest height in Grandfather Mountain, with an altitude of 5,964^{ft} (1,817^m). Three other peaks reach above 5,000^{ft} (1,525^m), and a dozen or more, most of them in North Carolina, are above 4,000^{ft} (1,220^m). The most striking topographic feature of the Blue Ridge is the great difference in slopes on its opposite sides, for it is steep on the eastern and gradual on the western slopes. The eastward-flowing streams have cut back into the mountain belt, and, having the advantage of a more direct course to the sea, have encroached upon the territory of the westward-flowing streams, and have robbed them of portions of their drainage basins.

The eastern Monadnocks and Piedmont Valleys.—The eastern Monadnocks form several groups of mountains along the extreme

¹ HAYES, C. WILLIS, The Southern Appalachians. National Geographic Magazine 1: 319.

eastern border of the mountain belt, which have been more or less completely isolated by the erosion of eastward-flowing streams. The most important are the Brushy, South, and Saluda Mountains.

The Unaka Range.—The Unaka Range may be divided into a northern and a southern division. The northern division unites in the region of Grandfather Mountain with the Blue Ridge. From this point due west sixty miles (96^{km}), an irregular mountain mass extends to Paint Rock on the French Broad River. Compared with the Blue Ridge, the Unaka Range reaches a considerably greater average altitude, and contains most of the higher peaks in the southern Appalachians. Not only are these mountains higher, but their slopes are steeper, and their outlines more angular and rugged. The Unakas are equally steep on both sides, and slopes with a descent from crest to stream of 4,000^{ft} (1,220^m) are not uncommon. Many spurs leave the central chain, and between them are deep V-shaped ravines.

Central mountain groups and valleys.—From a commanding position somewhere on the Unaka Range, there may be seen stretching to the east and south a confused aggregation of peaks, ridges, and domes. The cultivated valleys are generally hidden from view, and, except for an occasional clearing and the grassy “balds” on a few of the higher domes, the whole region appears to be covered with a forest mantle. The interior mountains rise to considerable elevations. A very large number of summits reach altitudes between 4,000 and 5,000^{ft} (1,220–1,525^m), and a few culminate above 6,000^{ft} (1,825^m). The Black Mountains contain the highest peaks of the Appalachian Mountains, and from Roan Mountain they appear as a huge elongated range, broken into elevated domes, while the range culminates in Mount Mitchell, 6,711^{ft} (2,045^m), the highest point east of the Mississippi and 425^{ft} (130^m) higher than Mount Washington. Between these groups, and forming a sort of platform above which they arise, are many broad valleys, commonest toward the head of the streams. Only the smaller streams are flowing at the level of these valleys. Down-stream toward the northwest the broad valleys are found to be more and more deeply cut, until

these occupy deep narrow gorges. The broad valleys must have been formed at base level, before the commencement of the gorge cutting, and they afford the best possible evidence that the altitude of the region in which they are found has been increased by elevation in comparatively recent times.

HYDROGRAPHY.

The waters falling upon the several parts of this future National Park find their way eastward to the Atlantic, or southward directly to the Gulf of Mexico, or to the Mississippi River and thence to the Gulf. The divide between the Atlantic and Gulf drainage follows the crest of the Blue Ridge. The eastward-flowing streams are pressing this divide gradually westward by the capture of territory from less favorably situated streams west of the divide. Northwest of the divide the streams flow at first in the high broad valleys, then in deepening channels, directly to the higher, more rugged Unakas, which they cut through in narrow gorges, emerging upon the Appalachian Valley, those south of New River draining their waters into the Tennessee River.²

PHYSIOGRAPHY AND GEOLOGY.

The history of this region, as far as it concerns this paper, begins with the Cretaceous period. At least two great cycles of erosion are recorded in the southern Appalachians, in which the surface of an old continent was worn down from a considerable altitude nearly to base level. Shortly after the close of the Carboniferous period, the entire southern Appalachian province was finally lifted above sea level, and its subsequent history is recorded in the land forms. Following this uplift was a long period, during which the region was subjected to the physiographic processes constituting gradation. Finally, toward the close of the Cretaceous period, the whole province was reduced to a nearly featureless plain, the Cumberland peneplain, relieved

² See Hydrography of the southern Appalachian Mountain region. Water Supply and Irrigation Papers. U. S. Geological Survey, nos. 62 and 63. 8vo, 190 pages. Washington. 1902. These two papers by Henry A. Pressey give systematic measurements of the streams in the southern Appalachian Mountain district, and other data of special interest to the ecologist.

only by a few groups of hills where the highest mountains now stand. After the processes of base leveling were nearly completed, that is, toward the close of the Cretaceous period, the region was again uplifted, but unequally, so that at the same time its surface was warped. The streams had become sluggish, but the effect of the uplift was to stimulate them to renewed activity,³ so that they began cutting upon the last-formed peneplain, a process in which they are still engaged.

PHYSIOGRAPHIC CHANGES INFLUENCING THE DISTRIBUTION OF
PLANTS.

Constant change must have taken place in the flora, through the physiographic shifts in the continent, which have been described as taking place in the region of the southern Appalachians. New species were appearing by the process of mutation. Other species were crowded for room by the change of level and the wearing away of strata to which they had adapted themselves, for "if we suppose that the earlier Mesozoic uplands were the seat of the existing dicotyledons, then by the lowering of the surface by gradual consumption of the interstream areas, these forms must have been brought into conflict with the ancient flora of the lowlands and thereby forced into a contest for supremacy."⁴ These changes in the physical condition of whole areas produced coincident changes in the constituent plants of the several ecologic regions. Xerophytes were replaced by mesophytes; mesophytes, by the wearing away of the soil and the formation of cliffs by xerophytes. Hydrophytes replaced mesophytes when an area became too wet for the tenancy of ordinary plants. Mesophytes replaced hydrophytes, as a lake area was robbed of its water by some newly encroaching stream. All of these changes were represented in the mountain region of North Carolina, and the plants involved in the readjustment to altered conditions were Cretaceous or Tertiary plants. With the development of the Cumberland peneplain, the forest covering, if one existed at that time (and we have no reason for

³ HAYES, The southern Appalachians, *loc. cit.* 330.

⁴ WOODWORTH, J. B., The relation between base leveling and organic evolution. The American Geologist 14: 231.

believing that a heavy forest did not exist at that early date), was a mesophytic one with the addition of representative herbaceous plants that have not been preserved.

With the uplift of this plain, followed by its planing down by streams, valleys and gorges were created, and rocky strata were exposed, which supported, as such physiographic formations support today, a xerophytic flora. The character of the rocky outcrop influences the particular kind of vegetation, so that we may have a different flora with the same exposure of light, heat, and moisture, if the rocky formations are different. This does not depend so much upon the chemical composition of two different strata, as shown by Cowles,⁵ but it is because one formation is further along in its life-history than is the other, so that the vegetation of the clay hill today may be seen on a sand hill in the future. With the widening out of the valley by erosion, and the slackening of the flow of any stream by the reduction of the elevations to base level, the xerophytes of the hillsides will be replaced by the mesophytes of the peneplain. The laws that control changes in the plant covering of a country are, therefore, plainly physiographic and edaphic, if the meteorologic conditions remain the same. We may have broad flood plains, hills, cañons, lakes, and swamps, depending upon the history of the ever-changing topography. Wherever hills are being eroded, rivers widened, waterfalls eliminated, lakes filled, or coastal plains enlarged, there is found a constant change in the plant societies, or a succession in definite order of plant groups. In any land which has undergone degradation from a mountainous topography to a peneplain, we ought to find a marked change in the organisms at the close of the cycle of denudation. In the first stages of change from original constructional topography, effects will be discernible. Sculptured slopes with ravines, sharp divides, and peaks cradle species and varieties by barriers which oppose ingress and egress.

In the progress toward final base leveling, the repeated diversion of the streams, or the reversals of drainage, are a constant

⁵ COWLES, H. C., The influence of underlying rocks on the character of the vegetation. *Bulletin American Bureau of Geography* 2:— [pp. 26]. Je and D 1901.

cause of changed conditions which Alfred Russell Wallace emphasizes as of importance in the modification of species.⁶ The cycle begins in a mountainous tract with least facility for migration of species, and ends in broad lowlands, which favor the easy migration and wide distribution of plants and animals.⁷

The distribution of plants in the region of the southern Appalachians demonstrates the above-mentioned facts. Kearney⁸ has called attention to the presence of a Lower Austral (austro-riparian) element in the flora of the mountains of North Carolina. Over one hundred species, which are most abundant and most widely distributed in the austro-riparian area, are known to occur in the mountains at an elevation of 1,000^{ft} (300^m) or more. Below that altitude the flora of the southern Appalachian region is mainly Carolinian, and the presence in its midst of numerous austro-riparian forms would be expected. The occurrence, however, of Lower Austral species at higher elevations in the midst of a chiefly transition flora is the noteworthy fact in the distribution of plants in the southern Appalachians. In studying this flora, one soon reaches the conclusion that it comprises two categories of species, which are markedly different, not only in their systematic relationships, present distribution, and past history, but even to a considerable degree in their ecologic constitution. Two types of plants may be distinguished: those of neotropic origin, which have in all likelihood made their first appearance in the Appalachian region in geologically very modern times, probably after the close of the glacial epoch; and those not of neotropic origin, which probably represent the more or less modified descendants of the flora that in later Eocene or Miocene time extended to high northern latitudes, represented in eastern North America by two closely allied species, one in the coastal plain, and the other in the Appalachian region.

In order to explain the facts in the case, botanists have had

⁶ WALLACE, A. R., *Darwinism*, chap. v.

⁷ WOODWORTH, J. D., The relation between base leveling and organic evolution. *The American Geologist* 14:217. 1894.

⁸ KEARNEY, The lower austral element in the flora of the southern Appalachian region. *Science N. S.* 12:831.

recourse to the movement of glaciers southward during the ice age. It appears to the writer that the alternation of cold and warm periods is not necessary to account for the facts described above. An attempt is made in what follows to outline an alternative hypothesis which appears to be a more satisfactory exposition of the case. The elevation of the southern Appalachian region from the Cumberland base level satisfactorily accounts for the differentiation of the corresponding mountain and coastal species. The species now found on the mountains adapted themselves to the higher elevations, and, being more plastic, were wrought upon by the forces which were and are at work in the gradation of the southern Appalachian region. For no fact in biology is better known than the capacity of some species to endure a wide range of physical conditions, while others are fatally sensitive to comparatively slight differences of environment. The modification of the species above mentioned was influenced by the rapid change in the physiography and topography of the country, and not by the glacial ice-sheet, which during a late geologic epoch covered the whole of North America. The oscillations of level are known to have taken place, and it is conceivable that the progenitors of the austro-riparian plants of the mountains and coastal plain, specifically identical, mingled when the country was a level peneplain, becoming differentiated as the elevation of the land became more marked. The distribution of plants which represent the characteristic flora of Eocene and Miocene times is thus accounted for.

We have then, in the physiographic changes which have taken place in this mountain region, an explanation of the peculiarities of the flora of the southern Appalachians, which displays certain anomalies of distribution and isolation of monotypic plants. The presence of *Hudsonia montana* Nutt. on the summit of Table Rock is thus explained.⁹ Table Rock is an undenuded remnant of a former peneplain, and it is likely that *Hudsonia montana* Nutt. was once more extended in its distribution, but has been isolated by the erosion of the larger part of the plain on which it formerly grew in abundance. *Dicentra*

⁹ Collected there by Dr. John K. Small.

eximia DC. is another illustration, growing in a rather restricted area in the Doe River Gorge, where the river cuts between Iron Mountain and Gap Creek Mountain, North Carolina. *Shortia galacifolia* Torr. & Gray, *Lilium Grayi* S. Wats. on Roan Mountain, *Buckleya distichophylla* Torr. on Paint Rock are examples of this same local distribution and isolation.

PHENOLOGIC DISTRIBUTION OF PLANTS.

Four kinds of plants with reference to their phenologic distribution may be distinguished in the vegetation of the forests of eastern North America; viz.: plants of boreal genera (Arctic, Hudsonian, Canadian species), plants of temperate genera (Alleghanian and Carolinian), plants of warmer temperate climate (austro-riparian), and neotropic genera.

Both boreal and temperate species bloom in the spring before they are shaded by the leafing trees, but for different reasons. The plants of temperate origin vegetate and blossom in the spring before the trees are in leaf, because, as a matter of light relationship, it is the only season in which the functions of these plants can be performed adequately, and this presupposes the influence of a certain number of heat units greater than for boreal species and less than for those of more southern origin. A more detailed statement on this subject will be made subsequently. The boreal plants, however, of the eastern Appalachian forests, blossom and vegetate early in the season, because that is the part of the year at which the development of these species, which require a minimum of heat units, is most adequately performed.¹⁰ The writer has shown this in a detailed manner in a paper published in *Science*.¹¹ The Scandinavian element of our flora consists of plants which mature their seeds quickly before the summer is well advanced. This marks them

¹⁰ The presence of many boreal plants in the forests and peat bogs of the northern states is accounted for by the encroachment of tree vegetation, after the glacial epoch, upon the areas occupied by the boreal plants, which surrounded by the trees, were destroyed or compelled to grow during the period when the trees are leafless. The movement of trees northward was occasioned by the fact that the land area, left bare by the retreat of the glaciers, was one of low tension, while the country to the south, as we have seen, was one of high tension.

¹¹ HARSHBERGER, The origin of our vernal flora. *Science* N. S. 1:92-98. Jan. 25, 1895.

as physiologically adapted to the influences of a previous short glacial summer. This rapid growth is insured by the activities of the plant during the previous short season in storing up large amounts of reserve material for the next brief season's growth. Even under favorable conditions of summer heat, every external perceptible vital motion in these boreal plants ceases, and it is only after a dormant period of some months, that growth can commence anew. This periodic alternation of vegetative activity and rest is in general so regulated that for a given species of plant both occur at definite times of the year, leading to the inference that the periodicity only depends upon the alternation of the seasons, and, therefore, chiefly upon that of temperature and moisture. The plants of Scandinavian affinity agree physiologically in having a periodic growth and rest. The following diagrams will illustrate this. Diagram *B*, if compared with diagram *A*, shows that the period of vegetative activity of our spring plants of boreal origin corresponds with an arctic or glacial summer, while the dormant period corresponds with an arctic winter, although our present summer has encroached on the former glacial winter.

A. ASTRONOMICAL YEAR DURING GLACIAL PERIOD.

VEGETATIVE PERIOD	FLOWERING AND REPRODUCTIVE PERIOD	DORMANT PERIOD	
GROWING PERIOD OF PLANTS			
ARCTIC SUMMER		ARCTIC WINTER	

B. ASTRONOMICAL YEAR — 1903.

VEGETATION	FLOWERS	DORMANT PERIOD	
GROWING PERIOD OF BOREAL PLANTS		DORMANCY OF SUMMER	DORMANCY OF WINTER
		←	→
PRESENT SUMMER		PRESENT WINTER	

The plants of warmer temperate climate (austro-riparian species) require a greater number of heat units than those plants just described, and their distribution at present depends largely upon temperature and soil conditions. In the case of the austro-riparian species found in the southern Appalachian mountains, two factors are probably most effective in permitting these species to maintain themselves in what would seem to be an unfriendly environment, viz., amount of insolation and the nature of the soil.¹²

A favorite situation in the mountains for colonies of lower austral species is on the southern exposure of hills, where the angle of inclination and the position with reference to the sun insure the greatest possible amount of insolation. The soil preferred by the great majority of these species is light, sandy, and poor in organic material; it is consequently readily permeable to water and becomes quickly and strongly heated, being thus similar to the soils which cover a great part of the coastal plain.

Unfortunately no phenologic data are at hand with reference to the plants of warmer temperate character. In lieu of exact data, a reference to Chapman's *Flora*¹³ may assist in determining the position of these plants with reference to the period of flowering. Those plants not of neotropic origin, which are probably the more or less modified descendants of that characteristic flora which existed in Eocene and Miocene times, and species of genera that appear to be on the wane, blossom in general, according to Chapman, from May to July, and are not looked upon as spring plants, which blossom from March until May. The neotropic element in the flora of the eastern United States is represented by plants that bloom in general from June until October,¹⁴ and are therefore summer and autumn species. This result of a phenologic tabulation of the austro-riparian plants might have been expected, when the origin and physio-

¹² KEARNEY, *loc. cit.* 841.

¹³ CHAPMAN, *Flora of the southern United States*. 3d ed.

¹⁴ Another group of plants, derived like the Cactaceae and Compositae from the southwest, bloom at about the same period as the plants of neotropic origin. See my paper in *Science*, *loc. cit.*

logic constitution of these plants is taken into consideration; for, according to the laws of temperature control of plants, species of neotropic and warm temperate origin need a large sum of heat units to carry on adequately their life-processes, and these are not properly carried on unless the specific number of heat units is provided in the environment.

INFLUENCE OF GLACIERS ON THE FLORA OF NORTH CAROLINA.

Upon the retreat of the ice-sheet, that portion of the continent north of the terminal moraine was tenanted again by plants that migrated northward, which as species were adapted to a cold temperate climate. A large number of these species came from the southern Appalachians and adjoining regions, where they had remained undisturbed in their original haunts during the long ice age, and were in a plastic condition for growth in a new environment, through the influence of the pressure of species upon each other in their southern home, and through the physiographic vicissitudes to which these fictile forms were subjected. Many species, therefore, growing in the North Carolina mountains, found congenial conditions in the more extensive land areas in the north.

An inspection of the forest maps to be found in the ninth volume of the Tenth Census Report, *Forest Trees of North America*, will show that there is a center of distribution which comprehends the area of the present states of southern and central Pennsylvania, West Virginia, Kentucky, Tennessee, western North Carolina, southwestern Virginia, northern Georgia, Alabama, Mississippi, where the largest number of species of the most important genera of North American deciduous trees will be found. A study of these maps reveals an important fact, that the spread of the species from this common center has been in a series of more or less concentric waves. Three waves may be distinguished. The first wave consisted of the distinctly glacial flora, which skirted the border of the ice-sheet. The second consisted of the present boreal forms, and the third was a wave of deciduous shrubs and trees, oaks, hickories, and a host of others. The species most successfully provided with means of distribution and most easily adjustable extended furthest

from the original home after the glacial epoch, which circumscribed the area of the original dense forest of the Miocene period. The outer confines of any particular genus is usually occupied, as shown in the maps, by a single species. Nearer the center two species are found; still nearer, if the genus is a large one, three, and still nearer four, etc. The position of the various shades of green on the maps suggests the circles of impulse produced when a stone is thrown into a basin of water. Theoretically these waves spread circumferentially in all directions, unless they meet with obstacles, when they are deflected. Similarly, the maps suggest a series of distributional impulses, by which the various species of oaks, ashes, hickories, and chestnuts were forced out from a parent forest of great density into the area left bare by the retreat of the great ice-sheet. The force which impelled this migration outward from the original forest, a relict of the continental forest of Miocene times, was the tension produced by the species associated together and in a struggle for supremacy, as regards room, light, etc. This struggle for existence must have been intense, as evidenced by the great size, height, and straightness of bole of the deciduous forest trees. Only two alternatives were left the species composing this original forest, namely, extinction or migration. Fortunately for the forest, an area of little or no tension was opened up upon the retreat of the glacial ice. The migration from an area of great tension has been and always will be toward an area of little tension.

MacMillan¹⁵ remarks on this point, with reference to the character of the Minnesota flora, that it has been shown that, while the valley of the Minnesota is geographically central, it is by no means botanically central, but, on the contrary, strongly southern and eastern. Bessey¹⁶ has shown that the trees and shrubs of Nebraska have come up the Missouri bottoms and spread from the southeastern corner of the state west and northwest. Mason states that the trees of Kansas show the same

¹⁵MACMILLAN, *The Metaspermae of the Minnesota Valley* 758, 759. 1892.

¹⁶BESSEY, *The forests and forest trees of Nebraska*. Ann. Rep. State Bd. of Agric. 1899:79-102.

origin. Adams¹⁷ has demonstrated this clearly in a study of the faunal distribution of animals and in a cursory way with plants.

The marshaling of these facts exhibits the flora of the southern Appalachians and of the mountains of North Carolina in a new light. That the plants of the northeastern and north central United States (except those left as high northern plants on the nunataks and non-glaciated islands and those of cold temperate habit) are derived from the region of the southern Appalachians, adds considerable zest to the study of the flora of these elevated mountain lands.

PRINCIPLES UNDERLYING THE DISTRIBUTION OF PLANTS IN EASTERN AMERICA.

It is advisable at this point to make a restatement of the principles underlying the distribution of plants in eastern America. These statements are derived from the work done by Gray, Hooker, and others on the distribution of North American plants, with additional facts which seem to the writer necessary to mention because of recent work that has been published with reference to the flora of North America in general.

1. Subsequent to the great Cretaceous uplift in a favorable period of mutation, the north temperate regions of Europe, Asia, and America which extended to high northern latitudes became the habitat of dicotyledons and monocotyledons identical as species in most important points.

This region was occupied by a forest of great density,¹⁸ composed of numerous species of trees, shrubs, and herbaceous plants, and these plants were subsequently definitely allocated during preglacial times to certain geographic areas by the planing down of the country to base level.

3. The movement of the glaciers southward over the north-

¹⁷ ADAMS, CHAS. C., Southeastern United States as a center of geographical distribution of flora and fauna. *Biological Bulletin* 3:115-129. Jl 1902.

¹⁸ GRAY, ASA, Sequoia and its history. *Proceedings American Association Advancement of Science* 21:1. 1872. *Scientific papers of ASA GRAY* 2:142; also *ibid.* 2:204. Cf. GRAY, Forest geography and archæology. *American Journal of Science* 16:85-94; 183-194.

land exterminated the plants of preglacial times without forcing a migration southward, except the northern herbs and trees left on the moraines, unglaciated islands, glacier margins, and nunataks of the great ice field.¹⁹

4. During the late Pleistocene, and also during the interglacial period, the Scandinavian element of the boreal and north temperate floras was introduced by the migration of plants from Scandinavia by the high northern roadway through northern Europe and Asia to North America, and, as shown, these plants remained on the retreat of the glaciers in the far north, and on the alpine summits of the more elevated mountains, or were held trapped in the cool shade of the north temperate forest or isolated in cold sphagnum bogs.

5. The plants of this north temperate region south of the terminal moraine during glacial times remained, on the retreat of the glaciers, in undisturbed possession of their original habitats. During the ice age they were still further reduced in numbers and influenced in their distribution by the physiographic forces constantly at work in the shaping of the continent.

6. Upon the retreat of the ice-sheet the glaciated area was supplied with plants from two main sources: (*a*) the plants that had maintained themselves in the north during the ice age, and (*b*) the contingent of plants supplied by the territory to the south and east.

7. Conclusively, therefore, the facts indicate the absence of a southern migration of plants.²⁰ Rather, they point to the glaciers as the important factor in the isolation of such botanic regions as eastern North America and eastern Asia, which perforce show affinities in their floral make-up that can be explained only by reference to the principles aforementioned.

¹⁹ WRIGHT and UPHAM, Greenland icefields and life in the north Atlantic 197-198. 1896.

RUSSELL, Glaciers of North America 86 and 117. 1897; also in Annual Report U. S. Geological Survey 13: 19-21. 1891-92.

WRIGHT, G. FREDERICK, The ice age in North America 57-62. 1891; also American Geologist 8: 330.

²⁰ This southern migration seems to the writer well-nigh impossible, because it would mean a movement from an area of lower tension to one of higher tension.

8. Following the glacial period the modification of the plants left in the several widely removed continental areas, eastern North America and eastern Asia, became accentuated, as time elapsed, until the similarities which are marked in the plants of preglacial times became less well defined and the differences evident in the two floras become the feature of recent times.

9. These facts argue for a great antiquity of the flora of the mountains of western North Carolina. The presence of so many peculiar types of plants, not found elsewhere in America and having their closest relatives in eastern Asia, makes it more certain that groups, now broken up and detached, were once continuous, and that fragmentary groups and isolated forms are but the relics of widespread types, which have been preserved in a few localities where the physical conditions were especially favorable, or where organic competition was less severe.

This important principle is evidenced on every hand as a botanist travels through western North Carolina. The large size of the trees, the close commingling in a dense forest of a great variety of species, the graded-down appearance of the land surface, and the rounded contour of the mountains, all impress the fact upon him that the country through which he travels has been subjected through long ages to the continued action of climatic forces which have carved the land into its present form and influenced the character of the vegetal covering. This impression is greatly heightened, if the following nine criteria for determining the centers of dispersal are applied to the study of the region in question:²¹

1. Location of greatest differentiation of type.
2. Location of dominance or great abundance of individuals.
3. Location of synthetic or closely related forms.
4. Location of maximum size of individuals.
5. Location of greatest productiveness and its relative stability.
6. Continuity and convergence of lines of dispersal.
7. Location of least dependence upon a restricted habitat.
8. Continuity and directness of individual variations, or modi-

²¹ ADAMS, CHAS. C., Southeastern United States as a center of geographical distribution of fauna and flora. *Biological Bulletin* 3 : 122.

fications radiating from the center of origin along the highways of dispersal.

9. Direction indicated by biogeographic affinities.

EDAPHIC FACTORS DETERMINING THE CHARACTER OF THE FLORA
OF WESTERN NORTH CAROLINA.

The soils of the higher mountains are rather fine and even-grained loams, gray or red in color, or black from organic ingredients; the loamy and generally stiffer subsoils are red or gray. Over the larger part of the area they are derived from the decomposition, *in situ*, of gneiss or gneissic schists, and are sufficiently deep for tree growth, particularly along the lower slopes. In portions of the region the soil derived from slates, quartzite, and metamorphosed sandstones are shallower, thinner, and not so favorable to tree growth.²² Soil, according to the definition of Professor Dokouchayev, a Russian investigator, is the superficial horizon of rocks in which the general processes and phenomena of weathering, transportation of particles, etc., combine with the biologic processes due to the influence of plants (lichens and alpine plants), animals, and micro-organisms, such as nitrifying bacteria.²³ A forest soil, such as we find in western North Carolina, is an expression, therefore, not only of the physico-geographic, geographic, and geophysics forces which have been brought to bear in its formation, but also of the geobiologic forces which have been at play. A study of any soil cannot fail to reveal many peculiarities of the vegetation that covers it, but it also throws a flood of light upon the succession of floras which may have flourished at any particular time in a given region. To elucidate: the soils of a given territory are influenced by the life-activities (instance the Leguminosae) and the dead remains of plants and other organisms (peat beds, humic compounds, animal manures, guano, etc.). The soil also influences the

²²PINCHOT and ASHE, Timber trees and forests of North Carolina. N. C. Geol. Surv. Bull. 6:220. 1897.

²³SIBIRTZEV, N., Genetic classification of soils. Zapiski Novo-Alexand. Inst. Selsk. Khoz. Lyesov. Memoirs of the Institute of Agriculture and Forestry at Novo Alexandria, Government of Lublin 9²:1-23. 1895. *Ibid.*, 11³:1-4. 1898. Experiment Station Record 12:705.

development and the life-activity of these organisms and their decomposition after death. The character of the plant growth, for example, plays not only a direct, but an intermediate rôle in the formation of soil. The relief of the soil has an important influence in determining the drainage, temperature, etc. And lastly, the successive changes which have taken place in the climate, the encroachments of the forests, the spread of marshes, the drying up of the soil, etc., must in their turn influence the character of soils. A knowledge of the laws and the forms of these influences makes it possible to obtain from the study of soils a basis for the reconstitution of the recent past of the country and for sketching its recent geophysics and geobiologic history. An inspection of the soils of western North Carolina reveals a close relationship between the vegetal covering and the soil. There are a number of humus dwellers with ectotrophic and endotrophic mycorrhiza. Such plants as the oaks, beeches, chestnuts, poplars, willows, pines, spruces, and firs are provided with ectotrophic mycorrhiza and therefore are to a certain extent dependent on the humus of the soil. Without it a dense forest could not exist, and in any region, such as the mountainous area of North Carolina, the luxuriance of the forest is a correlative of the richness of the soil in humus and its mechanical condition, and *vice versa*.²⁴ Plants with endotrophic mycorrhiza also add their quota to the upbuilding and maintenance of the forest litter, and so do many fungi. In North Carolina, as elsewhere, the rotten windfalls and the fallen leaves return many valuable ingredients to the earth. In the North Carolina mountains, if undisturbed by man, a deep soil rich in organic detritus is found, and this clearly points to the long occupation of the territory by dense forests.

These introductory remarks have been made to show the delicate balance which exists between the vegetation of western North Carolina, on the one hand, and the soil and physiographic features, on the other. Constant change has been manifested in

²⁴ Another indication of a soil rich in humus is a great variety of saprophytic fungi belonging to several well-recognized groups, such as the Polyporei, Agaricineae, etc.

the transformation that has been made from the monotonous plateau of early Cretaceous times, covered with a rather tame flora, to the richly diversified configuration of the mountains and plains of today, clothed with the most magnificent forests (excepting those of the Pacific slope) to be found anywhere in the western hemisphere. The ecologic disposition of the vegetation with reference to the topography next concerns us.

[*To be concluded.*]